

Is there a general trait of susceptibility to simultaneous contrast?

Article (Accepted Version)

Bosten, J M and Mollon, J D (2010) Is there a general trait of susceptibility to simultaneous contrast? Vision Research, 50 (17). pp. 1656-1664. ISSN 0042-6989

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/id/eprint/52519/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

Copyright and reuse:

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

Is there a general trait of susceptibility to simultaneous contrast?

Individuals differ in their susceptibility to simultaneous contrast. Are the underlying differences in neural machinery conserved across different stimulus dimensions? We measured the extent to which 97 subjects perceived simultaneous contrast on the dimensions of luminance, colour, luminance contrast, colour contrast, orientation, spatial frequency, motion and numerosity. Individual differences showed retest reliability for each dimension ($0.32 \leq \text{ICC}(c,1) \leq 0.78$, $p \leq 0.05$), but susceptibility to simultaneous contrast, with a few exceptions, was not correlated across dimensions. Either susceptibility to contrast arises empirically from an individual's interactions with the environment, or it is genetically determined but independently for different dimensions.

Many visual attributes exhibit simultaneous contrast. It occurs in stimuli embedded spatially in a related context: the appearance of the embedded stimulus is shifted away from that of the surround. Since simultaneous contrast across disparate stimulus dimensions may plausibly share a common neural mechanism, individuals who are particularly susceptible to one contrast effect may be particularly susceptible to them all. To address this possibility we studied individual differences in the extent to which simultaneous contrast is perceived across multiple stimulus dimensions. We measured susceptibility to simultaneous contrast across ten different stimulus dimensions: luminance contrast (Diamond, 1953), colour contrast, luminance contrast contrast (Chubb *et al.*, 1989), colour contrast contrast (Singer & D'Zmura, 1994), motion

contrast (Duncker, 1938), orientation contrast (Westheimer, 1990), spatial frequency contrast (Klein *et al.*, 1974) and numerosity contrast (MacKay, 1973; Durgin, 2002).

Explanations for simultaneous contrast have been offered within different frameworks and at different levels. One tradition, classically identified with Hering (1920), offers a physiological account, in terms of neural interactions. Another, classically identified with Helmholtz, offers a cognitive account in terms of the most likely interpretation of the scene. These different levels of explanation are not necessarily exclusive (Kingdom, 1997).

Recent physiological and anatomical approaches to simultaneous contrast have focused on extra-classical receptive fields. Extra-classical receptive fields are defined by the non-linear response to stimuli in the surround: a neuron's level of activation is modulated by a stimulus in its extra-classical receptive field only if there is a stimulus concurrently in its classical receptive field. The presence of extra-classical receptive fields shows that the neural machinery exists for an influence of spatial context. Their existence has been reported at many levels of the visual system including the retina (Cleland & Levick, 1974; Solomon *et al.*, 2006), the Lateral Geniculate Nucleus (LGN) (Levick *et al.*, 1972; Felisberti & Derrington, 2001), cortical area V1 (Maffei & Fiorentini, 1976; Fitzpatrick, 2000), and cortical area V5 (Allman *et al.*, 1985; Born, 2000). What neural circuitry gives rise to the extra-classical receptive field is still debated. Candidates are lateral connections (Das & Gilbert,

1999 on V1; Bodin *et al.*, 2005 on LGN), feedforward connections (Alitto & Usrey, 2008 on LGN) and feedback connections (Angelucci *et al.*, 2002 on V1; Nolt *et al.*, 2007 on LGN).

More than one tradition has sought an account of contrast in terms of the structure of the stimulus rather than the structure of the nervous system. Bayesian models interpret simultaneous contrast and other "illusions" as the product of the visual system's best guess at what an ambiguous retinal stimulus corresponds to in the external world (for a review see Schwartz *et al.*, 2007). A particular case of this class of explanation, and one with a long history, is the hypothesis that equates simultaneous contrast with constancy (Monge, 1789; Ikeda *et al.*, 2006; Mollon, 2006). Models put forward by Purves *et al.* (Purves & Lotto, 2001; Purves & Lotto, 2003) relate a constancy explanation of simultaneous contrast to a Bayesian approach more explicitly.

The study of individual differences is an under-used method of establishing relationships between different psychophysical measures (Wimler, 2008). In the present case, if individual differences were conserved across stimulus dimensions, a simple low-level explanation for simultaneous contrast would be favoured. If not, the neural mechanisms may differ between stimulus attributes or alternatively, the mechanism may be common but its degree of instantiation for different dimensions may vary. An absence of conserved individual differences would also be compatible with empirical models of simultaneous contrast. Individual differences in visual experience, either externally or internally generated,

could lead to differences in the ability to isolate elements of the visual field, or to different expectations about the configuration of objects that corresponds to the retinal image.

Little work has so far been carried out on individual differences in simultaneous contrast, but one exception has been in the dimension of luminance contrast contrast. Cannon and Fullenkamp (1993) categorised observers into three types, each type showing a characteristic pattern of response to contrast contrast stimuli. One type of observer consistently exhibited contrast suppression of the central test disc, no matter what the relative contrasts of centre and surround. Another type of observer showed some enhancement particularly for surrounds of small diameter and for central patches containing low contrast. A minority of observers fell into a third category, labelled 'enhancers,' who showed consistent enhancement of the contrast of the central test patch. Cannon and Fullenkamp used their results to explain simultaneous contrast by a combination of processes where components had different weightings in different individuals. Snowden and Hammett (1998) have also reported individual differences in perception of contrast contrast, and Dakin et al. (2005) have reported that schizophrenics are less susceptible to contrast contrast than are the normal population.

In the present study, as well as testing the relationship between different dimensions of simultaneous contrast, we quantify the range of individual variation in multiple types of simultaneous contrast, including luminance contrast contrast. We assess and report the re-test reliabilities for each dimension of simultaneous contrast.

Methods

To minimise the variance introduced by different task demands for different stimulus dimensions, the tasks were kept as similar as possible. All used asymmetric matching as a method, and the size and the configuration of the stimuli remained constant. Each of the ten stimulus dimensions was tested in a separate block and the blocks were run in random order. Within each block, two different test patch surrounds were tested (with the exception of numerosity contrast, see footnote to Table 1); elsewhere these will be referred to as measures 1 and 2, as listed in Table 1.

Stimuli

For all stimulus dimensions a circular test patch of diameter 3.1° was presented on one side of the screen and a comparison patch of the same diameter on the other. The test patch was embedded in an annular surround of diameter 12.40° , and the centres of the test and comparison patches were separated by 14° . The viewing distance was constant at 70 cm, maintained by positioning the subject on a chin rest. Figure 1 is a representation of the test patches and their surrounds for each stimulus dimension. The properties of all the stimuli used are given in Table 1.

A series of pilot studies determined the parameters for each stimulus dimension that led to the greatest levels of individual variation in susceptibility to simultaneous contrast (Bosten, 2008). In the case of two dimensions, the stimulus arrangement had features that need special comment:

Luminance

The stimuli were presented on a background of a high-contrast checkerboard (Zaidi *et al.*, 1997). The comparison patch is always potentially subject to simultaneous contrast with *its* surround. If black were chosen as its surround, then the contrast would be maximal and it would be difficult to match decremental test patches. If a mid-grey surround were chosen, then the comparison patch would disappear when it had the same luminance as the surround. The advantage of the checkerboard is that the average luminance of the comparison patch surround is a mid-grey, but the visibility of the comparison patch is preserved.

Motion

In the motion contrast display, the test patch was moving (leftward at 1 deg.s^{-1}) rather than stationary. This arrangement was adopted to minimise the problem that subjects can judge motion relative to different frames of reference. A subject might perceive the test grating as

moving relative to the moving surround but might perceive the test grating as stationary relative to the aperture caused by the border of the test patch. This ambiguity might make it difficult for the subject to judge the speed of the test grating. If the test grating is itself moving, it is in motion relative both to the moving surround grating and to its border, and the problem of contradictory percepts is thus reduced.

Stimuli were presented on a Sony GDM F500R graphics monitor, linearised using a Cambridge Research Systems ColorCal, and calibrated using a PR650 spectroradiometer. The monitor's refresh rate was 100 Hz, and its resolution was 1024 x 768. Experiments took place in a dark room. They were programmed in Matlab and were run using a Cambridge Research Systems VSG2/5 graphics card. Chromaticities are expressed in MacLeod-Boynton (1979) chromaticity coordinates.

Procedure

Subjects were instructed to indicate by pushbutton on each trial whether the test patch or the comparison patch was the greater on a particular perceptual dimension. The perceptual dimension varied according to the block and the participant indicated, according to the block, which of the test or comparison patches was lighter (luminance contrast), of higher contrast (luminance contrast contrast and colour contrast contrast), redder ($L/(L+M)$ colour contrast), more violet ($S/(L+M)$ colour contrast), faster in a leftward direction (motion contrast), of higher spatial frequency (spatial frequency contrast), rotated more anticlockwise (orientation contrast) or contained more dots (numerosity contrast). Before the first

experimental session, subjects received training on discriminating the stimulus dimensions that were the most difficult. These were the two types of colour contrast, orientation contrast, motion contrast and S/(L+M) contrast contrast. In the training blocks there were real differences between test and comparison patches, and the inducing surrounds were absent. Subjects were required to give ten consecutive correct responses on each training block before proceeding further.

Within each block there were four interleaved staircases, with the staircase to be tested on each trial decided according to a series of 4 x 4 Latin squares. Within each block the effects of two distinct surrounds were measured, and two staircases altered the comparison patch to converge on the subject's match to the test patch embedded in each surround. Staircases 1 and 2 converged on the subject's match when surround 1 was presented and staircases 3 and 4 when surround 2 was presented (see Table 1). Staircases 1 and 3 began at the same stimulus level greater than the veridical test patch match, and staircases 2 and 4 began at the same stimulus level lower than the veridical test patch match.

On each trial the test stimulus and comparison stimulus were presented for 3 s. The subject could give his or her response at any time during the stimulus presentation or during one second following. A 500-ms high tone marked the end of the response interval and a 500-ms low tone told the subject that the response had been recorded. The step size was variable, reducing after the second, third and fifth reversals on each staircase. The step sizes are given in Table 1. A condition terminated when there had been at least 14 reversals on each pair of staircases.

The entire experiment took subjects between 50 and 90 minutes and they completed the experiment twice in two sessions at least 6 weeks apart.

Subjects

The analysis is based on 97 subjects who completed both experimental sessions: 64 were female and 33 were male. A large proportion of subjects were graduate students at the University of Cambridge. Their ages ranged from 19 to 75, but 92% were under 40. All had normal or corrected-to-normal vision.

Analysis

A cumulative Gaussian psychometric function was fitted to the data from each pair of staircases in a block using the freely available software *psignifit* (Wichmann & Hill, 2001a, 2001b). The 50% point was read as the point of subjective equality from the function fitted by *psignifit*.

Exclusion criteria

Forty data points were gathered from each of the 97 subjects. Some data points were classed as "erroneous" according to one of three criteria. The first was that the pair of staircases used to measure a particular data point diverged rather than converged (0.875% of the data eliminated).

The second was that the subject appeared to be comparing the comparison patch with the test patch surround rather than the test patch itself (0.275% of the data eliminated). The third was that the 68% confidence intervals returned by *psignifit* (by bootstrapping with 5000 simulations) on the threshold estimate were greater than the range of the subjects' matches (1.125% of the data eliminated).

Other missing data points

20 data points (0.52% of the data) were lost at the point of collection owing to subjects' overrunning their allotted time or to system failures.

Results

Reliability

Reliability was established by correlating subjects' thresholds across the two experimental sessions. Intraclass correlation coefficients (C,1) for the 20 measures of simultaneous contrast ranged from 0.322 to 0.783. All were significant ($p < 0.05$ with a Bonferroni correction). Correlation coefficients and their 95% confidence intervals are given in Table 2. Significant correlations between the measures of simultaneous contrast taken in the first and second sessions indicated that there are reliable individual differences in all the measures.

Simultaneous contrast

No distribution of points of subjective equality was significantly different from normal ($0.444 \leq \text{Kolmogorov-Smirnov } Z \leq 1.786$; $0.0034 \leq p \leq 0.989$; with a Bonferroni correction for 20 tests, the alpha value was 0.0025). We tested each distribution of points of subjective equality for simultaneous contrast, defined as the value of the matched comparison patch being significantly different from the physical value of the test patch, in the direction away from the inducing surround. Significant simultaneous contrast effects were found in all but two measures ($3.79 \leq t \leq 24.82$; $p \leq 0.05$). The exceptions were S/(L+M) contrast contrast 1 and spatial frequency contrast 1. The mean, standard deviation and range for each measure of simultaneous contrast are given in Table 3.

Each set of points of subjective equality was tested for sex differences, but no significant differences were found either in the magnitude of simultaneous contrast ($0.035 \leq t \leq 2.1$; $p \geq 0.04$, $\alpha = 0.0025$), or in the variance of the points of subjective equality ($0.005 \leq F \leq 6.8$; $p \geq 0.01$, $\alpha = 0.0025$). Similarly, each set of points of subjective equality was correlated with subjects' ages. There were no significant correlations between age and magnitude of simultaneous contrast ($0.007 \leq r_p \leq 0.216$, $0.033 \leq p \leq 0.943$, $\alpha = 0.0025$).

Correlations between stimulus dimensions

Table 4 shows a matrix of correlations across all dimensions. The input to the correlation matrix was the points of subjective equality for each measure averaged for each subject across the two sessions, or from a single session if there was only one value available. The correlations are

colour-coded by magnitude. Those that are significant following a Bonferroni correction for 190 tests ($\alpha = 0.00026$) are indicated in yellow. Lower correlations ($p < 0.01$) are indicated in green, and correlations that are lower still ($p < 0.05$) are indicated in blue. The most striking result is that susceptibility to simultaneous contrast does not generally correlate across stimulus dimensions: if a subject is particularly susceptible to one type of simultaneous contrast, he or she is not necessarily particularly susceptible to other types. Most correlation coefficients are very low indeed: 27.9% of coefficients are below 0.05 and 53% of coefficients are below 0.1. The preponderance of low correlations means that a factor analysis is inappropriate.

There are a small number of exceptions to the trend of low correlations: 13 correlations (6.5%) are significant. Eight of these are intercorrelations between the three measures of contrast contrast ($0.394 \leq r_p \leq 0.721$; $4.6 \times 10^{-5} \leq p \leq 1.9 \times 10^{-17}$). The others are between the two measures of spatial frequency contrast ($r_p = 0.374$, $p = 0.0001$), between the two measures of numerosity contrast ($r_p = 0.469$, $p = 8.6 \times 10^{-7}$), between L/(L+M) contrast and S/(L+M) contrast where the test patches were decrements ($r_p = 0.397$, $p = 4.4 \times 10^{-5}$), between luminance contrast and S/(L+M) contrast contrast ($r_p = 0.364$, $p = 0.0002$) and between L/(L+M) contrast contrast and spatial frequency contrast ($r_p = 0.376$, $p = 0.0001$).

The fact that the number of significant correlations is small is not, alone, very surprising. With 100 subjects and the necessity of performing a Bonferroni correction for 190 tests (lowering alpha to 0.00026), our study had sufficient power to detect only large effect sizes. Power calculations revealed that with an alpha of 0.00026, and 100 subjects we could expect to find a correlation of $r_p = 0.43$ with a power of 80%. However, statistical power depends not only on sample size, alpha value and effect size, but also on the level of noise present in the data. In other words, the *true* correlation between two variables is weakened in the *observed* correlation by the level of noise present in the measurements of each variable. The following equation allows estimation of the "true" correlation given the observed correlation and the reliabilities of each of the two correlated variables X and Y:

$$r_o = r_t / (R_x R_y)^{1/2} \quad (1)$$

where r_o is the observed correlation, r_t is the "true" correlation, and R_x and R_y are the coefficients of reliability for the variables X and Y¹.

¹ The coefficient of reliability is the proportion of variance that is shared across the two or more sessions of measuring the variables X and Y. When we are measuring the reliability of individual differences, the numerator of this ratio is the variance attributable to true individual differences. The total variance (the denominator of the ratio) is the sum of the variance attributable to true individual differences and the variance attributed to random error (or noise).

Since the correlations between dimensions of simultaneous contrast were performed using the data averaged across two sessions, we used the intraclass correlation coefficient (c,1) for the average of two measures to give us the coefficients of reliability for each dimension. We were then able to estimate the minimum expected "true" correlations given 80% power, 100 subjects and an alpha value of 0.0026 from equation (1). These ranged, depending on the reliabilities for each measure of simultaneous contrast, from 0.5 to 0.78. The true power of our study to detect significant correlations, was therefore limited to large effect sizes.

It is more informative to look at the distribution of all 190 correlations between our 20 measures of simultaneous contrast. If there were such a thing as a general trait of susceptibility to simultaneous contrast, we should expect the distribution of correlations to be centred on the mean observed effect size. The distribution of the 190 correlations between measures of simultaneous contrast is shown in Figure 2. Because on some scales a large amount of simultaneous contrast would reveal itself by reduced scores whereas on others a large amount of simultaneous contrast would give enhanced scores (see Table 1), if there were a general trait of susceptibility to simultaneous contrast, we should expect the correlations between some measures of simultaneous contrast to be positive and others to be negative. We therefore reflected the correlations we expected to be negative about the line $r_p = 0$ before including them in Figure 2.

The distribution of observed correlations (red, Figure 2) includes many correlations that are negative (even following the transformation described above), and many that are zero or near-zero. The mean of the distribution is 0.081, its standard deviation is 0.17, and its peak is at 0 with histogram bins of width 0.05. An estimate of the distribution of "true" correlations may be obtained by transforming the distribution of observed correlations according to equation 1. The distribution of projected "true" correlations is shown in Figure 2 in blue. The distribution's mean is 0.11, its standard deviation is 0.23 and its peak is at 0-0.1.

How do the distributions of observed and "true" correlations compare with distributions of correlations among variables consisting entirely of random noise? To answer this question we ran Monte Carlo simulations correlating random pairs of data points rather than data points gathered from the same subjects. One hundred simulations from random permutations were made and the results are also shown in Figure 2. The solid black line shows the average distribution of correlations across all the simulations, and the dashed lines show the maximum and minimum number of correlations of each level that occurred in any simulation. The Monte Carlo simulation can be compared with the observed and estimated "true" distributions of correlations shown in red and blue, respectively. It is clear from the figure that the observed distribution of correlations overlaps largely with the distribution expected by chance, but there is a positive arm of the distribution that falls outside the distribution expected by chance. The number of positive correlations falling outside the distribution expected by chance is increased, as would be expected, when the "true" correlations are estimated.

Discussion

Although there are significant differences in susceptibility to simultaneous contrast apparent in each individual measure, this susceptibility, with few exceptions, does not give rise to significant correlations between measures. The three measures of contrast contrast intercorrelate significantly, and $S/(L+M)$ contrast and $L/(L+M)$ contrast are correlated significantly when surrounds in both cases had a higher value than the test patch. Few other dimensions of simultaneous contrast intercorrelate significantly.

The distribution of the 190 correlations obtained between our measures of simultaneous contrast indicates that many correlations between measures of simultaneous contrast are negative or near-zero. An estimation of the distribution of "true" correlations has shown that a general effect, existent, must be very small ($r_p \leq 0.11$). There may be a very small general trait of susceptibility to simultaneous contrast, accounting for around 1% of the variance in each measure. However, a subset of correlations are larger: some dimensions of simultaneous contrast intercorrelate better than others, for example, the different measures of simultaneous contrast contrast.

What can be concluded from the general absence of correlations between individuals' settings on different dimensions of simultaneous contrast?

One basic conclusion is that there is no noteworthy general trait of susceptibility. It thus seems unlikely that individual differences in all the

different dimensions can be accounted for by conserved variation in one neural property such as the density or the extent of lateral connections or the gain control exercised by synapses on postsynaptic cells or the spatial precision of descending attentional processes that allow a particular region of the visual field to be isolated. Our results do not rule out the possibility that individual differences in contrast on particular dimensions are caused by variations in such neural properties: genetic polymorphisms or environmental influences might determine the operating parameters of neural mechanisms that are essentially similar – for example, the growth of lateral connections could be terminated at different developmental points in different visual subsystems and this timing could be different for different individuals. But our results would also be consistent with empirical accounts that attribute simultaneous contrast to learnt expectations about the visual world. Such learning would be free to progress independently in different individuals for each stimulus dimension.

Acknowledgements: Supported by a Gatsby Foundation Grant to J Mollon, R Durbin and G Mitchison. J Bosten was a Medical Research Council research student.

Figure Legends

Table1: *Stimulus parameters.*

Table 2: *Intraclass correlation coefficients (C, I) for the first and second sessions for each measure, with 95% confidence intervals. With a Bonferroni correction for 20 tests, the adjusted alpha value is 0.0025.*

Table 3: *Mean, standard deviation and range of points of subjective equality for each measure of simultaneous contrast.*

Table 4: *Pearson's Correlations between dimensions of simultaneous contrast.*

Figure 1: *Stimuli for simultaneous contrast. From top left: $L/(L+M)$ contrast, $S/(L+M)$ contrast, $L/(L+M)$, $S/(L+M)$, luminance contrast, luminance, motion, numerosity, orientation and spatial frequency.*

Figure 2: *Distributions of observed and “true” correlations, and the range of distributions of correlations expected by chance. The distribution of observed correlations between measures of simultaneous contrast is shown in red, with those expected to be negative reflected about $r_p = 0$. The distribution of calculated “true” correlations is shown in blue. The results of Monte-Carlo simulations to determine the distribution of*

correlations expected from random noise are indicated by the black lines. The mean of 100 simulations is indicated by the solid black line, and the maximum and minimum number of correlations of each level that occurred in any simulation are indicated by the black dashed lines.

Alitto H & Usrey W (2008). Origin and Dynamics of Extraclassical Suppression in the Lateral Geniculate Nucleus of the Macaque Monkey. *Neuron* **57**, 135-146.

Allman J, Miezin F & McGuinness E (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception* **14**, 105-126.

Angelucci A, Levitt J, Walton E, Hupe J, Bullier J & Lund J (2002). Circuits for local and global signal integration in primary visual cortex. *Journal of Neuroscience* **22**, 8633-8646.

Bodin V, Mante V & Carandini M (2005). The Suppressive Field of Neurons in Lateral Geniculate Nucleus. *The Journal of Neuroscience* **25**, 10844-10856.

Born R (2000). Center-surround interactions in the middle temporal visual area of the owl monkey. *Journal of Neurophysiology* **84**, 2658-2669.

Bosten J (2008). Contrast and Constancy in Visual Perception, Unpublished doctoral dissertation. University of Cambridge.

Cannon MW & Fullenkamp SC (1993). Spatial Interactions in Apparent Contrast: Individual Differences in Enhancement and Suppression Effects. *Vision Research* **33**, 1685-1695.

Chubb C, Sperling G & Solomon J (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Science of the USA* **86**, 9631-9635.

Cleland B & Levick W (1974). Brisk and Sluggish Concentrically Organized Ganglion Cells in the Cat's Retina. *Journal of Physiology* **240**, 421-456.

Dakin S, Carlin P & Hemsley D (2005). Weak suppression of visual context in chronic schizophrenia. *Current Biology* **15**, R822-R824.

Das A & Gilbert CD (1999). Topography of contextual modulations mediated by short-range interactions in primary visual cortex. *Nature* **399**, 655-661.

Diamond AL (1953). Foveal Simultaneous Brightness Contrast as a Function of Inducing- and Test-field Luminances. *Journal of Experimental Psychology* **45**, 304-314.

Duncker K (1938). Induced motion. In *A Source Book of Gestalt Psychology*. ed. Ellis W, pp. 161-172. Harcourt, Brace and Company, New York.

Durgin F (2002). Lateral Interactions of Texture Density (Kurtosis). *Investigative Ophthalmology and Visual Science* **43**, E-Abstract 2912.

Felisberti F & Derrington AM (2001). Long-range interactions in the lateral geniculate nucleus of the New-World monkey, *Callithrix jacchus*. *Visual Neuroscience* **18**, 209-218.

Fitzpatrick D (2000). Seeing beyond the receptive field in primary visual cortex. *Current Opinion in Neurobiology* **10**, 438-443.

Hering E (1920). *Translation 1964; Outlines of a Theory of the Light Sense*, Cambridge, MA.

Ikeda M, Pungrasamee P, Katemake P & Hansubesai A (2006). The Brain Adaptation to the Color of Illumination and not the Retinal Adaptation to the Color of Objects that Determines the Color Appearance of an Object in Space. *Optical Review* **13**, 388-395.

Kingdom F (1997). Simultaneous contrast: the legacies of Hering and Helmholtz. *Perception* **26**, 673-677.

Klein S, Stromeyer III CF & Ganz L (1974). The simultaneous spatial frequency shift: A dissociation between the detection and perception of gratings. *Vision Research* **14**, 1421-1432.

Levick W, Cleland B & Dubin M (1972). Lateral geniculate neurons of cat: Retinal inputs and physiology. *Investigative Ophthalmology* **11**, 302-311.

MacKay DM (1973). Lateral Interaction between Neural Channels sensitive to Texture Density? *Nature* **245**, 159-161.

MacLeod DIA & Boynton RM (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America* **69**, 1183-1186.

Maffei L & Fiorentini A (1976). The Unresponsive Regions of Visual Cortical Receptive Fields. *Vision Research* **16**, 1131-1139.

Mollon JD (2006). Monge. *Visual Neuroscience* **23**, 1-13.

Monge G (1789). Mémoire sur quelques phénomènes de la vision. *Annales de Chimie* **3**, 131-147.

Nolt M, Kumbhani R & Palmer L (2007). Suppression at High Spatial Frequencies in the Lateral Geniculate Nucleus of the Cat. *Journal of Neurophysiology* **98**, 1167-1180.

Purves D & Lotto B (2003). *Why We See What We Do*. Sinaur Associates, Ltd., Sunderland, MA.

Purves D & Lotto RB (2001). Why We See Things the Way We Do: Evidence for a Wholly Empirical Strategy of Vision. *Philosophical Transactions of the Royal Society of London, Series B* **356**, 285-297.

Schwartz O, Hsu A & Daya P (2007). Space and time in visual context. *Nature Reviews Neuroscience* **8**, 522-535.

Singer B & D'Zmura M (1994). Color Contrast Induction. *Vision Research* **34**, 3111-3126.

Snowden RJ & Hammett ST (1998). The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. *Vision Research* **38**, 1935-1945.

Solomon SG, Lee B & Sun H (2006). Suppressive Surrounds and Contrast Gain in Magnocellular-Pathway Retinal Ganglion Cells of Macaque. *The Journal of Neuroscience* **26**, 8715-8726.

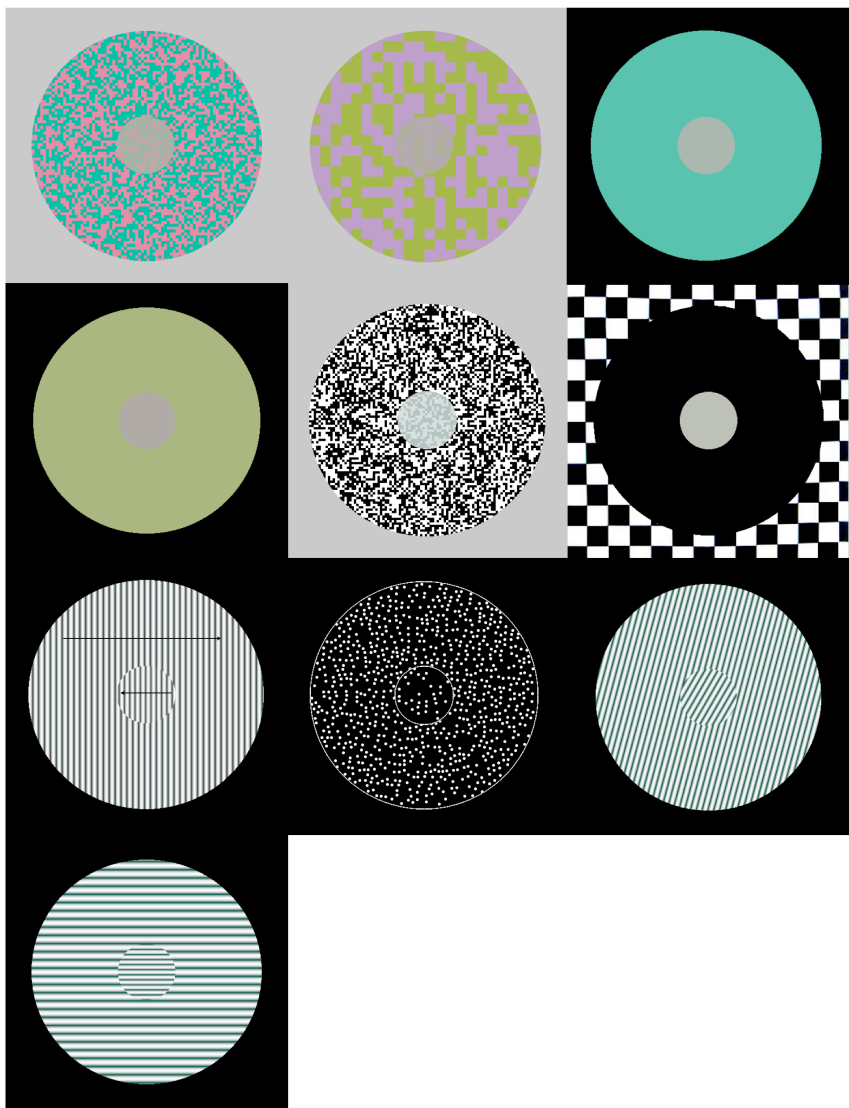
Westheimer G (1990). Simultaneous orientation contrast for lines in the human fovea. *Vision Research* **30**, 1913-1921.

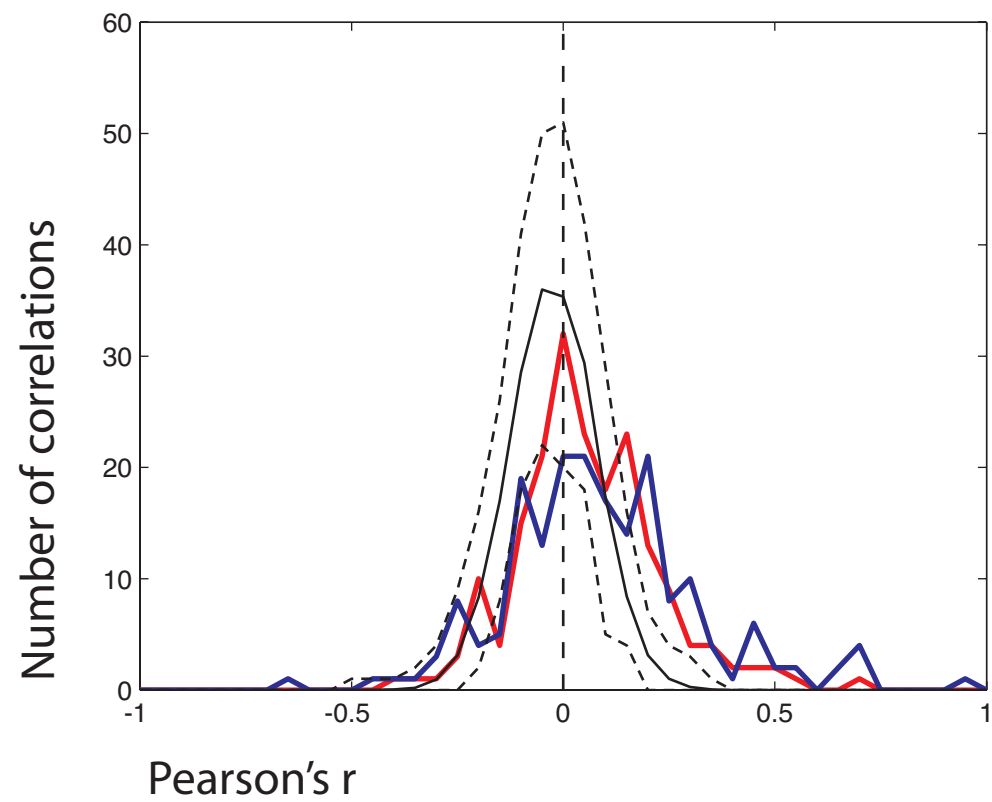
Wichmann FA & Hill NJ (2001a). The psychometric function: I. Fitting, sampling and goodness of fit. *Perception and Psychophysics* **63**, 1293-1313.

Wichmann FA & Hill NJ (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception and Psychophysics* **63**, 1314-1329.

Wimler J (2008). How to use individual differences to isolate functional organization, biology and utility of visual functions; with illustrative proposals for stereopsis. *Spatial Vision* **21**, 561-579.

Zaidi Q, Spehar B & Shy M (1997). Induced effects of backgrounds and foregrounds in three-dimensional configurations: the role of T-junctions. *Perception* **26**, 395-408.





Type of simultaneous contrast	L/(L+M) contrast	S/(L+M) contrast	L/(L+M)	S/(L+M)	Luminance contrast	Luminance	Motion	Numerosity	Orientation	Spatial Frequency
Units	Equivalent of Michelson contrast	Equivalent of Michelson contrast	L/(L+M)	S/(L+M)	Michelson contrast	cd.m ⁻²	cycles.s ⁻¹	dots	Degrees	c.p.d.
Starting position of staircases 1 and 3	0.090	0.75	0.641	0.01126	0.4	34.58	-1	12	40	2.63
Starting position of staircases 2 and 4	0	0	0.689	0.02086	0.096	62.56	1	45	80	6.06
Step size 1	0.0090	0.075	0.006	0.0012	0.048	2.33	0.2	8	5	0.1 log unit
Step size 2	0.0072	0.06	0.0048	0.00096	0.024	1.17	0.1	4	3	0.06 log unit
Step size 3	0.0036	0.030	0.0024	0.00048	0.012	0.58	0.1	2	2	0.04 log unit
Step size 4	0.0011	0.015	0.0012	0.00024	0.006	0.29	0.05	1	1	0.02 log unit
Test patch	0.045	0.37	0.665	0.0161	0.25	48.57	1	1) 30; 2) 53*	60	4
Surround 1	0.081	0.75	0.702	0.0233	0.6	97.14	2	800*	75	6.50
Surround 2	0.054	0.46	0.629	0.00879	0.3	38.86	-2	800*	45	2.46

Other parameters:										
Spatial frequency							3.6 c.p.d.		3.5 c.p.d.	
Contrast							~100%		~100%	
Grating orientation							Vertical			Vertical
Maximum luminance	18.3 cd.m ⁻²	18.3 cd.m ⁻²	18.3 cd.m ⁻²	18.3 cd.m ⁻²		97.1 cd.m ⁻²	97.1 cd.m ⁻²	97.1 cd.m ⁻²	97.1 cd.m ⁻²	97.1 cd.m ⁻²
Minimum luminance	18.3 cd.m ⁻²	18.3 cd.m ⁻²	18.3 cd.m ⁻²	18.3 cd.m ⁻²		<0.01 cd.m ⁻²	<0.01 cd.m ⁻²	<0.01 cd.m ⁻²	<0.01 cd.m ⁻²	<0.01 cd.m ⁻²
Average luminance					48.6 cd.m ⁻²					
Dot diameter								0.16°		
Background dimensions	30° x 22.7°	30° x 22.7°			30° x 22.7°	30° x 22.7°				
Background chromaticity	Equal energy white	Equal energy white								
Check dimensions						0.65° x 0.65°				
Element size in contrast contrast	0.14° x 0.14°	0.49° x 0.49°			0.14° x 0.14°					

* Note that in the case of numerosity contrast, there was only one background dot density but the density of dots in the test patch varied. The numbers of test patch dots were 30 and 53, and this equated to dot densities of 3.97 and 7.02 dots per square degree of visual angle. The number of dots in the background was 800, and this was a dot density of 7.06 dots per square degree of visual angle.

Type	ICC(c,1) Single measures	p	n	Lower bound of 95% confidence interval on ICC(C,1)	Upper bound of 95% confidence interval on ICC(C,1)
L/(L+M) contrast 1	0.437	< 0.0001	92	0.256	0.589
L/(L+M) contrast 2	0.677	< 0.0001	96	0.552	0.772
S/(L+M) contrast 1	0.577	< 0.0001	95	0.425	0.697
S/(L+M) contrast 2	0.625	< 0.0001	95	0.486	0.733
L/(L+M) 1	0.687	< 0.0001	92	0.561	0.781
L/(L+M) 2	0.712	< 0.0001	92	0.595	0.800
S/(L+M) 1	0.669	< 0.0001	84	0.532	0.772
S/(L+M) 2	0.641	< 0.0001	86	0.497	0.750
Luminance contrast 1	0.614	< 0.0001	94	0.470	0.726
Luminance contrast 2	0.470	< 0.0001	96	0.298	0.612
Luminance 1	0.782	< 0.0001	92	0.688	0.851
Luminance 2	0.680	< 0.0001	92	0.553	0.776
Motion 1	0.741	< 0.0001	91	0.632	0.821
Motion 2	0.666	< 0.0001	83	0.527	0.771
Numerosity 1	0.450	< 0.0001	91	0.269	0.599
Numerosity 2	0.471	< 0.0001	92	0.295	0.615

Orientation 1	0.530	< 0.0001	87	0.630	0.666
Orientation 2	0.591	< 0.0001	87	0.435	0.712
Spatial frequency 1	0.321	0.001	94	0.127	0.491
Spatial frequency 2	0.616	< 0.0001	93	0.472	0.728

Type	Units	Mean point of subjective equality	Standard Deviation	Range
L/(L+M) contrast 1 contrast 1	Equivalent of Michelson contrast	0.0298	0.00596	0.0110 - 0.0453
L/(L+M) contrast 2 contrast 2		0.0353	0.00690	0.0114 - 0.0622
S/(L+M) contrast 1 contrast 1	Equivalent of Michelson contrast	0.334	0.107	0.0530 - 0.842
S/(L+M) contrast 2 contrast 2		0.327	0.0707	0.0556 - 0.573
L/(L+M) 1	L/(L+M)	0.660	0.00450	0.647 - 0.670
L/(L+M) 2		0.671	0.00474	0.662 - 0.683
S/(L+M) 1	S/(L+M)	0.0137	0.00144	0.00921 - 0.0165
S/(L+M) 2		0.0169	0.00149	0.0135 - 0.0226
Luminance contrast 1	Michelson contrast	0.190	0.0434	0.103 - 0.354
Luminance contrast 2		0.196	0.0283	0.083 - 0.249
Luminance 1	cd.m ⁻²	40.2	4.71	25.3 - 54.3
Luminance 2		56.9	5.13	47.4 - 69.0
Motion 1	cycles.s ⁻¹	0.643	0.292	-0.711 - 1.73

Motion 2		1.20	0.515	-0.615 - 2.37
Numerosity 1		25.2	1.98	18.2 - 30.1
Numerosity 2	dots	49.0	2.93	42.7 - 60.1
Orientation 1		54.3	4.26	44.7 - 64.7
Orientation 2	degrees	67.8	4.80	56.3 - 79.9
Spatial frequency 1		3.94	0.205	3.28 - 4.83
Spatial frequency 2	c.p.d.	4.11	0.260	3.40 - 4.91

		L/(L+M) contrast contrast 2	S/(L+M) contrast contrast 1	S/(L+M) contrast contrast 2	L/(L+M) 1	L/(L+M) 2	S/(L+M) 1	S/(L+M) 2	contrast contrast 1	contrast contrast 2	luminance 1	luminance 2	motion 1	motion 2	numerosity 1	numerosity 2	orientation 1	orientation 2	spatial frequency 1	spatial frequency 2
L/(L+M) contrast 1	r p N	0.538 8.01E-09 100	0.458 1.62E-06 100	0.408 2.52E-05 100	0.161 0.112 99	-0.133 0.191 99	0.182 0.070 100	-0.057 0.574 100	0.412 2.06E-05 100	0.216 0.03106 100	0.196 0.052 99	-0.001 0.989 99	-0.007 0.941 100	-0.143 0.158 99	0.120 0.237 99	0.112 0.272 99	0.040 0.691 100	-0.117 0.246 100	0.376 0.000113 100	0.286 0.00390 100
L/(L+M) contrast 2	r p N		0.394 4.65E-05 101	0.574 3.60E-10 101	0.111 0.273 100	0.000 0.999 100	0.109 0.277 101	0.077 0.446 101	0.270 0.00641 101	0.519 2.74E-08 101	0.193 0.054 100	-0.171 0.089 100	-0.082 0.414 101	-0.016 0.875 100	0.082 0.417 100	0.045 0.659 100	0.025 0.803 101	-0.170 0.090 101	0.206 0.0390 101	0.330 0.000745 101
S/(L+M) contrast 1	r p N			0.721 1.85E-17 101	0.049 0.627 100	-0.106 0.295 100	0.067 0.503 101	0.055 0.585 101	0.238 0.0163 101	0.084 0.402 101	0.364 0.000197 100	0.154 0.127 100	0.038 0.704 101	0.084 0.406 100	0.086 0.393 100	0.234 0.0189 100	0.089 0.377 101	0.183 0.0677 101	0.327 0.000858 101	0.187 0.0610 101
S/(L+M) contrast 2	r p N				-0.025 0.808 100	0.027 0.791 100	0.043 0.668 101	0.000 0.998 101	0.156 0.118 101	0.332 0.000685 101	0.276 0.00536 100	-0.086 0.396 100	0.018 0.856 101	0.066 0.512 100	0.111 0.271 100	0.160 0.113 100	0.045 0.654 101	0.106 0.291 101	0.277 0.00502 101	0.206 0.0383 101
L/(L+M) 1	r p N					-0.100 0.320 100	0.397 4.41E-05 100	0.045 0.655 100	0.132 0.191 100	-0.034 0.740 100	0.183 0.069 99	0.189 0.060 99	0.114 0.259 100	-0.044 0.667 99	-0.160 0.114 99	-0.058 0.568 99	0.065 0.522 100	0.015 0.879 100	0.016 0.876 100	-0.047 0.645 100
L/(L+M) 2	r p N						-0.309 0.00175 100	0.124 0.737 100	-0.034 0.737 100	0.235 0.0186 100	-0.240 0.0165 99	-0.034 0.735 99	-0.205 0.0403 100	0.060 0.556 99	-0.043 0.676 99	-0.043 0.674 99	0.076 0.453 100	-0.077 0.449 100	-0.173 0.085 100	-0.054 0.994 100
S/(L+M) 1	r p N							-0.014 0.223 101	0.0249 0.612 101	-0.0511 0.612 101	0.2086 0.0373 100	0.1273 0.207 100	0.0101 0.920 101	0.0945 0.670 100	-0.0431 0.691 100	0.0403 0.691 100	0.0256 0.799 101	-0.1241 0.216 101	0.0703 0.485 101	0.0008 0.994 101
S/(L+M) 2	r p N								-0.144 0.151 101	0.053 0.599 101	-0.300 0.00245 100	0.050 0.622 100	-0.221 0.115 101	0.128 0.205 100	-0.158 0.115 100	-0.173 0.085 100	-0.054 0.594 101	0.038 0.706 101	-0.153 0.125 101	0.098 0.331 101
Luminance contrast 1	r p									0.295 0.00272	0.298 0.00264	-0.032 0.755	0.019 0.852	-0.055 0.588	0.220 0.0275	0.169 0.092	0.150 0.133	-0.175 0.080	0.281 0.00446	0.047 0.644

	N
Luminance contrast 2	r p N
luminance 1	r p N
luminance 2	r p N
motion 1	r p N
motion 2	r p N
numerosity 1	r p N
numerosity 2	r p N
orientation 1	r p N
orientation 2	r p N
spatial frequency 1	r p N

	p<0.000263, significant
	p<0.001
	p<0.05

101	100	100	101	100	100	100	101	101	101	101
	0.0216 0.831 100	-0.2515 0.0116 100	-0.2017 0.0431 101	0.0218 0.830 100	0.1523 0.130 100	0.1066 0.291 100	-0.0743 0.460 101	-0.1903 0.057 101	0.0216 0.830 101	0.1418 0.157 101
		0.150 0.135 100	0.095 0.346 100	-0.067 0.507 99	0.031 0.763 99	-0.050 0.626 99	0.089 0.379 100	0.158 0.115 100	0.212 0.0346 100	0.143 0.156 100
			0.178 0.0767 100	0.281 0.00477 99	-0.171 0.090 99	-0.154 0.128 99	0.050 0.622 100	0.089 0.381 100	0.058 0.563 100	-0.078 0.442 100
				0.024 0.815 100	0.002 0.981 100	-0.166 0.099 100	-0.040 0.691 101	-0.018 0.856 101	0.290 0.00322 101	-0.064 0.522 101
					0.036 0.723 99	0.037 0.714 99	-0.160 0.111 100	0.076 0.454 100	-0.223 0.0256 100	-0.189 0.060 100
						0.469 8.6E-07 100	0.0123 0.904 100	-0.169 0.0929 100	-0.0502 0.620 100	0.00569 0.955 100
							-0.013 0.346 100	-0.095 0.396 100	-0.086 0.396 100	-0.121 0.231 100
								-0.204 0.0409 101	0.169 0.091 101	-0.029 0.774 101
									-0.077 0.442 101	-0.034 0.733 101
										0.374 0.000116 101